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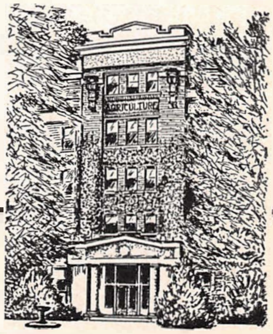

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Studies of the Olfactory Behavior of the Douglas-fir Beetle, *Dendroctonus pseudotsugae* Hopkins

O. K. JANTZ AND J. A. RUDINSKY

INTRODUCTION

Recognition of the destructive capabilities of the Douglas-fir beetle, *Dendroctonus pseudotsugae* Hopkins, and its impact on timber management and logging practices has stimulated expanded research with this species. Direct control has met with limited success and only temporary loss reduction in the presence of factors favorable for population increase of this beetle. The function of scent cues in population dispersal, host finding, and reproduction has only recently been realized, but now valuable data concerning population size, flight habits, ecology, and longevity can be obtained by the use of attractants. Bark beetles have developed a highly specialized sense of smell. Knowledge of their behavioral responses opens a new and relatively unexplored means of control. Baited traps can also facilitate a survey program by delineating areas of known infestation and by finding new ones. Greater economic importance of attractants in preventing or controlling epidemics, moreover, can be expected as soon as synthesized active material can be developed.

Early investigations on the Douglas-fir beetle revealed the existence of a secondary attraction made by the gallery-initiating female. Causes of attraction to the host and olfactory behavior during this host selection and subsequent attack remained to be investigated.

The work reported here concerns the behavioral responses exhibited by the Douglas-fir beetle to various attractant sources. Field and laboratory studies revealed response differences during different types of locomotion. The investigation also included a histological examination of the beetle digestive tract in an attempt to locate the site of pheromone production.

LITERATURE REVIEW

Various phases of the biology of the Douglas-fir beetle have been studied and control has been demonstrated under certain limited situations (*3,. 13, 23, 26, 29*).[1] Like most scolytids, the Douglas-fir

[1] Numbers in parentheses refer to References Cited, page 36.

beetle spends nearly 12 months within its host. The beetle has a one-year life cycle with two broods per generation. Two distinct overwintering groups of the beetle are found in coastal regions near Corvallis, Oregon. Overlap occurs in emergence and attack of the two groups. The first attack made by the overwintering new adults and parent adults begins in late March or during April, with a peak flight occurring the middle part of May, and continues in decreasing numbers until mid-June. Broods resulting from this initial attack develop to form the callow or teneral adults, those sexually immature beetles whose exoskeleton is still relatively soft with a bronze color. These beetles turn black while overwintering and are ready to take part in the spring attack the next year.

The second or summer attack period begins approximately in the middle of June and continues through July; this attack results from a combined effort of new adults which have matured from overwintering larvae together with a portion of those adults which reemerge after having made an initial spring attack. Broods resulting from the second attack overwinter, as a rule, in the larval stage. After development during the following spring, these beetles will join in the second or summer attack of that year.

Interest in attractants has increased recently because of the possibility that they may provide an answer to the problems of insect resistance to insecticides and pesticide residues.

Chemical communication among insects is common (*11, 15, 19, 20, 25, 45*). Although the literature shows isolated references to "swarming" of beetles (*4, 17, 28*), the first important experiment proving that a secondary attraction is produced by the invading beetles was that of Anderson (*1*) in 1948 with *Ips pini* Say. Studies with *Ips confusus* (LeConte) (*46, 47*), *Dendroctonus brevicomis* LeConte (*44*), *D. ponderosae* Hopkins (formerly *monticolae*) (*44*), and *D. pseudotsugae* Hopkins (*35*) substantiate the "mass attack" phenomenon.

Recently, significant advances have been made in research concerning the behavior of the Douglas-fir beetle. It has been shown by Rudinsky (*34, 35*) and McMullen and Atkins (*31*) that the attractive substance responsible for mass invasion is produced by sexually mature, unmated females feeding on suitable host material. Subsequent to emergence, and in the absence of fresh windthrow in the area, a dispersal flight occurred at random which later became a concentrated flight in response to the attraction caused by unmated females. The concentrated flight toward centers of attraction revealed distinct diurnal and seasonal patterns (*35*).

Fundamental studies on the Douglas-fir beetle have tried to explain the general causes of rise and fall in population levels. Consider-

able data have accumulated on its flight behavior (*2, 6, 10*). Considering the vastness of the forest, adverseness of environmental conditions, and size of the beetle, this flight period warrants considerable attention.

The equipment necessary to standardize observations on the bark beetle populations in flight and the numbers drawn to the release of attractants have been tested and amply discussed (*12*). Vité and Gara (*41*) discuss the difficulties with laboratory olfactometers and the problem of duplicating results in the field. Duplication would be impossible with certain species, since flight exercise is necessary prior to a release of chemotropic response (*14*).

Numerous theories have emerged to explain how bark beetles locate suitable host material in the vicinity of abundant, apparently unsuitable trees. The often-discussed "host selection principle" proposed by Hopkins (*18*) has frequently been tested. This principle states that a species which breeds in two or more hosts will prefer to continue to breed in the host to which it has become adapted.

The behavior patterns associated with host selection are complex. Various insect groups may have a different sequence in the chain of reactions during the selection process and may respond to different attractive components.

The initial invasion of several species is believed to be at random when there are no fresh windthrown or cut trees present in the area (*35, 36, 47*). Males initiate the galleries in some cases (genus *Ips*) and females in other instances (genus *Dendroctonus*).

In order to more nearly explain this host factor complex, considerable effort has been exerted with respect to tree physiology. Rudinsky and Vité (*37*) studied the water conduction pattern in conifers to more fully understand the plant's conquest of a new environment. They later concluded (*43*) that the reason certain trees resist bark beetle attack while others succumb must be physiological in nature, caused by disturbances in water relations. Studies along this line, particularly with ponderosa pine, continue to show that tree predisposition to bark beetle infestation is linked to disturbances in water relations which decrease the turgidity of the cells (*40, 44*). Vité (*40*) shows how the oleoresin exudation pressure is directly related to water stresses in the tree.

The limited studies on attraction of oleoresins add a new dimension to bark beetle-tree relationships. Injured trees bear an abnormal risk of attack due to low oleoresin exudation pressures. Chararas (*8*) surmises that physical conditions such as sunlight and relative humidity play an important role in determining susceptibility of trees toward certain scolytids. His studies reveal that certain fractions of oleoresins, pinene and limonene, show an optimum percentage at 1 to 3%

for five scolytid species. Earlier he had shown (*7*) that alpha pinene, beta pinene, and terpineol, all repellent in high concentrations, are attractive in dilute concentrations: 3 to 5% for *Ips typographus,* 2 to 3% for *Hylurgops palliatus* Gyll., and 1 to 2% for *Dryocoetes autographus* Ratzeburg. In 1961, Chararas and Berton (*9*) noted that in the oleoresins of coniferae, the concentration of terpenes, which is directly related to the vitality of the infested tree, plays a major part in attracting the scolytids. Numerous volatile substances which may include both essential oils and volatile acids are present in wood. Frequently their composition is exceedingly complex (*27*). Vapors of pine resins have been shown to be toxic to some species of bark beetles (*38*), while raw oleoresin attracts others (*42*).

The Douglas-fir beetle, *Dendroctonus pseudotsugae* Hopkins, is considered the most destructive insect enemy of its major host, Douglas-fir, *Pseudotsugae menziesii* (Mirb.) Franco. Even under latent population levels this beetle causes continuous, although usually unspectacular, mortality to its chief host in the intermountain region (*30*).

Insecticidal control or removal of infested logs is impractical because the infested area is often inaccessible when the insect kills single trees or scattered groups of trees around isolated windthrow nuclei.

It has been found (*24*) that freshly felled Douglas-fir attracts Douglas-fir beetles which, once in the area, will attack nearby living trees, as well as downed material. This attraction to freshly felled material points to a new approach in reducing losses caused by this insect.

MATERIAL AND METHODS

Marys Peak watershed, the field experimental area, is located within the Siuslaw National Forest approximately 20 miles west of Corvallis, Oregon. The approximate elevation of the experimental plot is 1,200 feet on a northeastern slope. It is composed mostly of second growth Douglas-fir trees and associated conifers. Grand fir, *Abies grandis* (Dougl.) Lind., western hemlock, *Tsuga heterophylla* (Raf.) Sarg., and western red cedar, *Thuja plicata* Donn., are present in limited numbers.

Field and laboratory tests were designed to observe olfactory responses of the Douglas-fir beetle. Results were compared with collections from nonselecting mechanical sweep nets and with diurnal and seasonal emergence patterns.

For laboratory testing, unmated females were introduced into the bark of recently cut logs of Douglas-fir; grand fir; western hemlock;

western white pine, *Pinus monticola* Dougl.; ponderosa pine, *Pinus ponderosa* Laws; western larch, *Larix occidentalis* Nutt.; black cottonwood, *Populus trichocarpa* Torr. and Gray; and Oregon white oak, *Quercus garryana* Dougl. Female beetles boring in xylem (debarked log), plasterboard, plywood, and empty holes in Douglas-fir served as checks. Jantz and Rudinsky have recently described their techniques using male beetles to assay for responses to volatile substances. Arrestment of beetles crawling over these substances was used a a criterion for response (*22*). The beetles crawling over a screen covering the test material were arrested, or did not stop, or turned back, i.e., were repelled.

An additional method of observing olfactory responses in the laboratory involved the use of a multiple choice, arena-type olfactometer. Air passing over a volatile substance resulted in a directed response by the insect as opposed to the passive arrestment. All tests in the arena-type olfactometer were conducted in total darkness. Emerged beetles were tested in groups of 50, with 15 minutes exposure time.

Resinous materials tested included oleoresin collected from xylem of Douglas-fir and ponderosa pine, Douglas-fir phloem extracts, Douglas-fir rosin, oleoresin fractions of pine (alpha pinene, beta pinene, limonene, and myrcene), and female boring-dust extracts. Tests with additional terpenes (camphene, geraniol, and alpha-terpineol) are presented elsewhere (*36*).

A histological examination of various stages of both male and female beetle digestive tracts was undertaken in an attempt to locate the region responsible for the production of an attractant. Transverse serial sections, 10 microns thick, were cut of the various alimentary canal regions. Comparisons between sexes were made of mature unmated beetles before and after feeding, while additional sections included those from females of callow adult, mated, reemerged, and post-mature beetles. The callow adult beetles were taken from field galleries in July and were part of the brood from the spring attack. Reemerged beetles were those parent adults which had emerged from logs caged after initial spring attack of the current season, and post-mature beetles were parent adults taken from field galleries after mating and egg deposition. The brood from which the post-mature parent adults were taken consisted of third and fourth instar larvae. Three replicates of each stage were sectioned; however, many more beetles were dissected and examined for morphological differences of reproductive organs and accessory glands.

Dissections were performed in a physiological saline solution. After dissection, the tissues were immediately placed in Bouin's fixative for 12 to 18 hours, then dehydrated in dioxane and embedded in

paraplast tissue media. Sections were stained in Harris hematoxylin with eosin-Y as a counterstain.

Field experiments were designed to measure olfactory responses of flying beetles. Rotary nets similar to those designed by Gara (*12*) were used for nonselective sampling. For selective sampling and bioassay of attractants in the forest, field olfactometers were used (*42*). The metal olfactometer includes a cylindrical base to house the baited material. Above this, a small blower powered by a portable generator draws air upward over the bait, releasing the volatile substance. Pegboard or plastic plates intercept flying beetles, which then fall into a jar attached to a wire funnel suspended from the top of the olfactometer (Figure 1). Olfactometers were spaced from 100 to 130 feet apart to prevent interference of compounds.

Screen cages (2 feet x 2 feet x 5 feet) fitted to a pressboard base were baited with female-infested logs and used extensively throughout the forest. Forty females were introduced into the inner bark of each log. Sexes were separated using the method described by Jantz and Johnsey (*21*).

Temperature and humidity were recorded continuously during the flight period by hygrothermographs in both the open area and under closed canopy. Dwyer wind meters were used to record significant changes in air movement.

Diurnal and seasonal emergence records were obtained by caging Douglas-fir logs infested during the previous season. Reemergence records of adult beetles were recorded by emergence from caged logs infested during the current flight season.

Field attraction by logs of various tree species, attack, and subsequent brood development were studied. Three replicates of six log species (Douglas-fir, western larch, ponderosa pine, western white pine, grand fir, and western hemlock) were placed two to three yards from highly attractive cages baited with Douglas-fir beetle females, and were considered to be within the perimeter of an attractant source. Three additional replicates were placed at distant points, 30 to 35 yards from any known attraction centers in the same general research area, and were considered to be outside the perimeter of attraction. All logs were placed in the field on April 6, 1963, three weeks prior to the first recorded Douglas-fir beetle flight period, and final results were recorded on September 4, 1963.

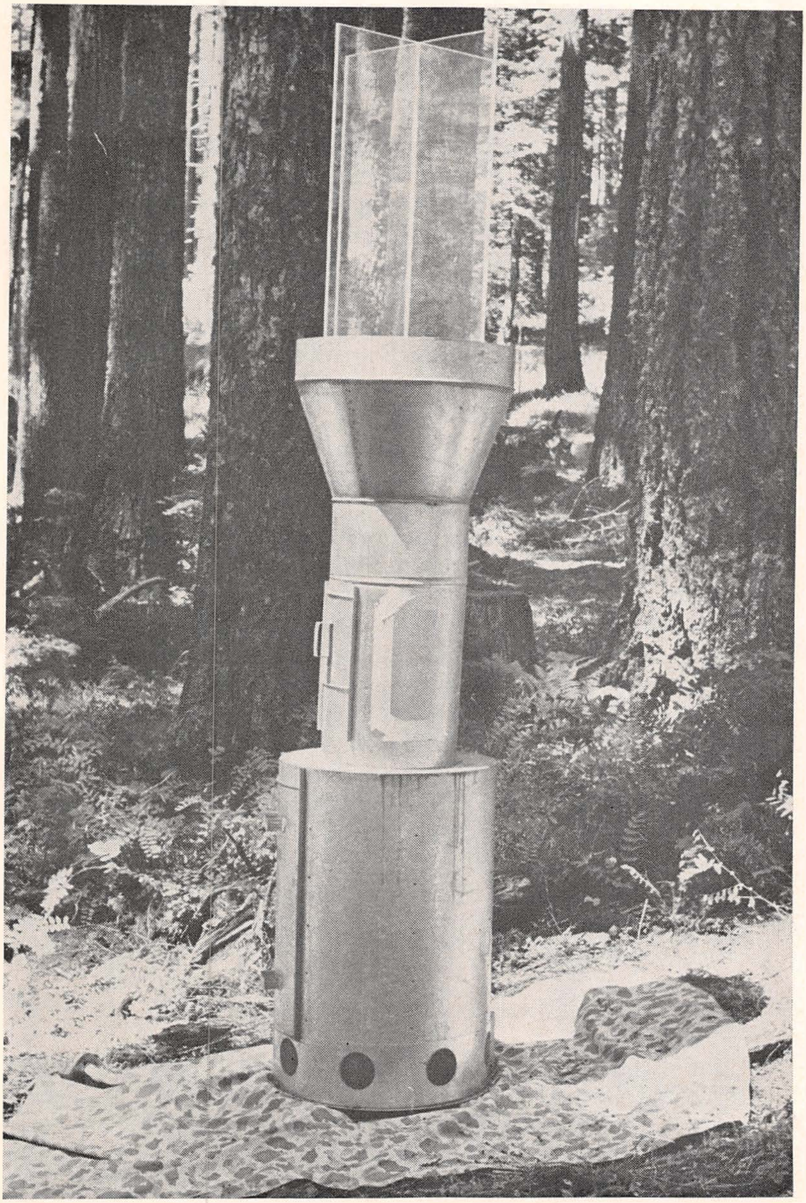

Figure 1. Metal olfactometer used for selective sampling and field testing of volatile materials.

RESULTS AND DISCUSSION

Laboratory Experiments

Arrestment

A recent report has shown that field populations do respond to the attraction produced by females boring in western hemlock, grand fir, and ponderosa pine (*16*). Additional work designed to determine basic differences in insect response during different types of locomotion has been reported. Jantz and Rudinsky found that beetles crawling in the laboratory did not exhibit a directed response to attractive materials without the presence of an air stream passing over the material toward the insect (*22*). Beetles were arrested while crawling near an attractant source, indicating that the threshold of response for crawling beetles is substantially different from that for flying beetles. Considering the delimited area within which arrestment of crawling beetles occurs, the concentration of the attractive substance directly above the screen under which the female is boring is probably greater than the concentration encountered by flying beetles. Thus, the threshold of response is higher for crawling beetles since they must be so near the source to respond. Flying beetles often orient to very weak stimuli, which indicates a low threshold level of response.

Results of arrestment tests with extract materials show Douglas-fir oleoresin to be repellent at all concentrations tested. Working as a survival mechanism, the volatile fractions from oleoresin (when diluted sufficiently by air) attract the beetles in flight to fresh, favorable logs, but repel crawling beetles within their immediate proximity.

Beetles confined with Douglas-fir resin in sealed containers, but not in direct contact with it, began to die in three days, while beetles sealed in air alone began to die in nine days. In identical tests using ponderosa pine oleoresin, death was recorded on the second day. Beetles completely engulfed by either Douglas-fir or ponderosa pine resin succumbed within one minute. All beetles were tested in the absence of food at 80° F.

Attraction

Of those materials tested in an olfactometer, males responded best to Douglas-fir and grand fir extracts prepared from borings made by the unmated females. There were no apparent responses to Douglas-fir oleoresin, rosin, and practical pinene. Numbers recorded for female beetles were not sufficiently greater than check samples to be classed as a response.

These results correspond with field attraction studies on various log species, i.e., response being greater on Douglas-fir than on grand fir and virtually nonexistent on western hemlock.

Histology of the alimentary canal

The objectives of this histological study were to see whether morphological structures or changes occur in the Douglas-fir beetle digestive tract which could be related to the production of an attractant.

The typical appearance of representative sections of both male and female alimentary canals is shown in Figure 2. Apparent differences exist between different stages of both female (Figure 2, A-C) and male (Figure 2, G-H) midguts. The most striking difference lies in the appearance of epithelial cells in the midgut of a newly emerged female (Figure 2, A) as compared to a male (Figure 2, G), since the female possesses an excessive amount of expanded, spongy cells. A definite change is noted in both sexes after feeding (Figure 2, B, H), but is most conspicuous in the female. The change after feeding indicates a return of the epithelial cells to a normal resting position after having discharged the cell contents into the ventriculus lumen. Figure 2, C, shows the cells expanding again to the original position.

In the genus *Ips* the polygamous male beetle selects new host material and after a period of feeding in the subcortical tissue produces an attractant. In contrast, in the genus *Dendroctonus,* the monogamous female beetle selects new host material and after a period of feeding on the inner bark produces an attractant. Therefore, in the case of the Douglas-fir beetle, if histological differences exist in connection with the production of an attractant, they would be expected in the female beetle. Thus, the question arises, can the differences observed in the midgut be interpreted in connection with the production of attraction or are they merely digestive processes? Pitman and Vité show histological differences in the ileum of the hindgut of *Ips confusus* and have suggested the existence of a type of holocrine secretion (*32*). Subsequent investigations, however, have been reported which indicate that the Malpighian tubules may also play a role in pheromone production (*33*). Figure 2, D-F and I-J, indicates that differences between various stages of the hindgut of both sexes of the Douglas-fir beetle are not apparent. Since Pitman and Vité have reported only on the hindgut, a comparison between midguts of the two genera is not possible at this time.

The digestive cells of the ventricular epithelium constitute the functional portion of the stomach. Their appearance varies greatly according to the state of the digestive processes. Snodgrass (*39*) divides the activities of the ventricular epithelium into four classes: (1) secretion and absorption; (2) excretion; (3) degeneration and regeneration of the digestive cells accompanying or following secretion; and (4) periodical delamination and replacement of the entire epithelium, mostly accompanying moults.

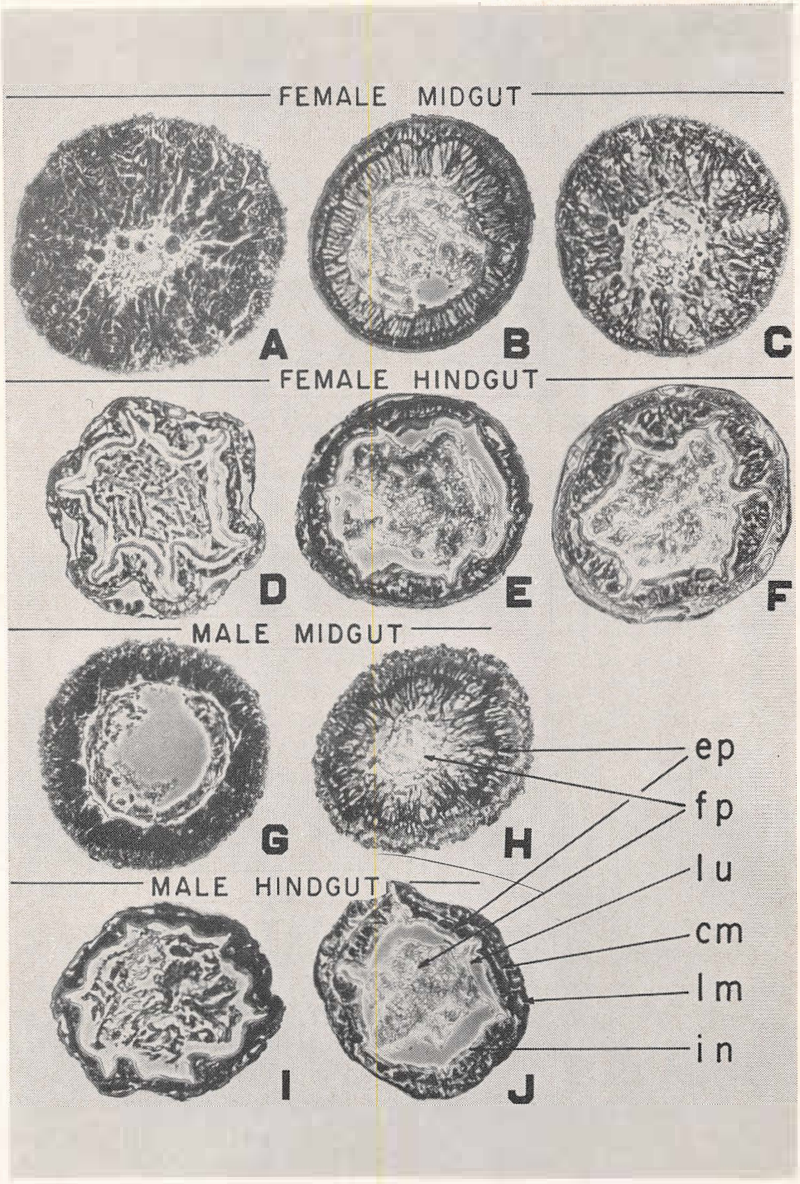

Figure 2. Transverse sections of the Douglas-fir beetle digestive tract. A, D, G, I — before feeding; B, E, H, J — 72 hours after initial feeding; C, F — after feeding, mating, and egg deposition. Ep = epithelial cells; fp = food particles; lu = lumen; cm = circular muscles; lm = longitudinal muscles; in = intima.

The conspicuous process of budding from the inner ends of the epithelial cells (Figure 2, A) of the female midgut is similar to that described by Snodgrass (*39*). He states that this form of disintegration, in which the cell given off contains a nucleus, results in a rapid and extensive depletion of the digestive cells of the epithelium. In most insects the buds are formed prior to feeding, and in the case of odonate larvae they may increase enormously in size and number in starved individuals (*39*). If this process is associated only with digestion, the same phenomenon would be expected in males, yet this was not apparent in the current studies (Figure 2, G).

Dissection of beetles at various time intervals from one day up to eight weeks after initial attack revealed the presence of food particles within both the midgut and hindgut. Therefore, the process of digestion apparently is a continuous one, and a complete and rapid exhaustion of digestive cells would not be expected.

Differences in freshness of host cambium, qualitative and quantitative changes in carbohydrate content, or other changes resulting from oxidative and fermentation processes would not be expected to have a significant effect on the insect in 72 hours or less. Whether the differences shown in the female midgut, before and after feeding, are associated with the origin of an attractant was not investigated (Figure 2, A-B).

Changes that existed in the reproductive organs and accessory glands could not be correlated with the attraction produced.

Field studies show that attraction is at a maximum two to three days after initial attack. The first few days after attack determine whether or not the beetle will be successful in establishing a brood. Under outbreak conditions, when attacks occur in standing trees, a concentration of beetles is necessary to overcome tree resistance. Under normal conditions, although tree resistance may not be involved, mating must be assured. Since attraction stops or drops to a low level after mating (Table 6), an initial, rapid expulsion of the attractant seems likely.

Attraction stops abruptly after mating, and very little residue is exhibited in the borings around entry holes. Either the compound is extremely volatile, requiring continuous production to be effective, or an exterior, cuticular-type secretion is involved. Further studies are suggested along this line considering the membranous lobes of the abdomen as a possible source.

Field Experiments

Patterns of emergence

Seasonal activities of the Douglas-fir beetle follow spring emergence, which is regulated by environmental conditions.

Development and maturation of the Douglas-fir beetle are directly influenced by temperature. External spring activity begins when maximum temperatures exceed the activity threshold, and this threshold varies between seasons. The maximum temperatures required to initiate daily emergence within a season decrease as the season advances (Table 1).

Table 1. INNER BARK TEMPERATURES IN RELATION TO EMERGENCE OF *Dendroctonus pseudotsugae* HOPKINS AT DIFFERENT TIMES OF THE SEASON

Time	March 8, 1963[1]		May 13, 1963	
	Inner bark	Emerged	Inner bark	Emerged
	° *F.*	*No.*	° *F.*	*No.*
0800	....	0	45	0
0900	55	0	46	0
1000	51	0	49	1
1100	58	0	50	6
1200	72	0	52	3
1300	76	0	54	9
1400	69	0	54	17
1500	73	0	55	3
1600	72	0	56	7
1700	65	0	55	1
1800	....	0	55	0
	March 29, 1964		May 11, 1964	
0900	....	0	50	0
1000	....	0	51	0
1100	54	0	53	4
1200	56	0	54	6
1300	59	0	56	21
1400	60	0	58	34
1500	61	0	59	38
1600	62	0	59	20
1700	63	0	57	3
1800	62	0	57	0

[1] Recorded in clearcut area; recorded in forested areas on the other three dates.

The decrease in threshold temperature required for emergence is directly related to the physiological condition of the beetle. When early season development is not complete, there is no stress or pres-

sure to emerge and fly. Later in the season when development is complete, and after initial emergence has begun, the beetles are under stress to emerge, but low temperatures will delay activity. Table 1 shows that temperature is not the limiting factor to initial emergence in early spring. On March 8, 1963, a temperature of 76° F. failed to initiate emergence. In contrast, on May 13, 1963, emergence was recorded at an inner bark temperature of 49° F. Similarly, in 1964, emergence occurred on May 11 at a subcortical temperature of 53° F., while on March 29, a temperature of 63° F. failed to initiate emergence, although spring emergence had begun in some areas.

Time and temperature required to initiate spring emergence vary considerably between seasons. If early spring temperature is favorable, the advanced development results in an early emergence as opposed to that during a less favorable season. The temperature at which initial emergence begins would then be lower than that required during a season with a less favorable development period, since beetles may already be under pressure to emerge and fly.

The first recorded emergence in the clearcut area in 1963 was on March 19 at a maximum air temperature of 57° F. (Figure 3). In 1964, emergence began eight days later at a five-degree higher temperature (Figure 4). Assuming equal bark thickness, early spring temperatures apparently were more favorable in 1963, allowing rapid advanced development. This appears to contradict the above discussion that emergence temperature decreases as the season advances; however, that situation refers only to those cases where the beetles are already physiologically mature and spring emergence has begun.

On March 29, 1964, a maximum daily temperature of 64° F. in the forested area did not cause emergence (Figure 4). However, after having begun, emergence was recorded at temperatures 12 degrees lower, and the peak emergence for that year occurred at a maximum daily temperature of only 63° F.

Figures 3 and 4 show a comparison between emergence in clearcut and forested areas in relation to maximum daily air temperatures for 1963 and 1964. Due to the radiant energy absorbed and the rapid increase in subcortical temperatures from direct exposure to the sun, early emergence in clearcut areas would be expected. In 1963, emergence in the forested area began 40 days after that in the clearcut area, while in 1964 a delay of 23 days occurred. The effect of direct exposure to the sun can be seen in a comparison of inner bark temperatures between logs in clearcut and forested areas (Table 2). On May 16, 1963, inner bark temperatures increased rapidly in the clearcut area obtaining an excess of 28 degrees over outside air temperature. In contrast, a gradual increase of inner bark temperature in the forested area never exceeded outside air temperature (Table 2). The ef-

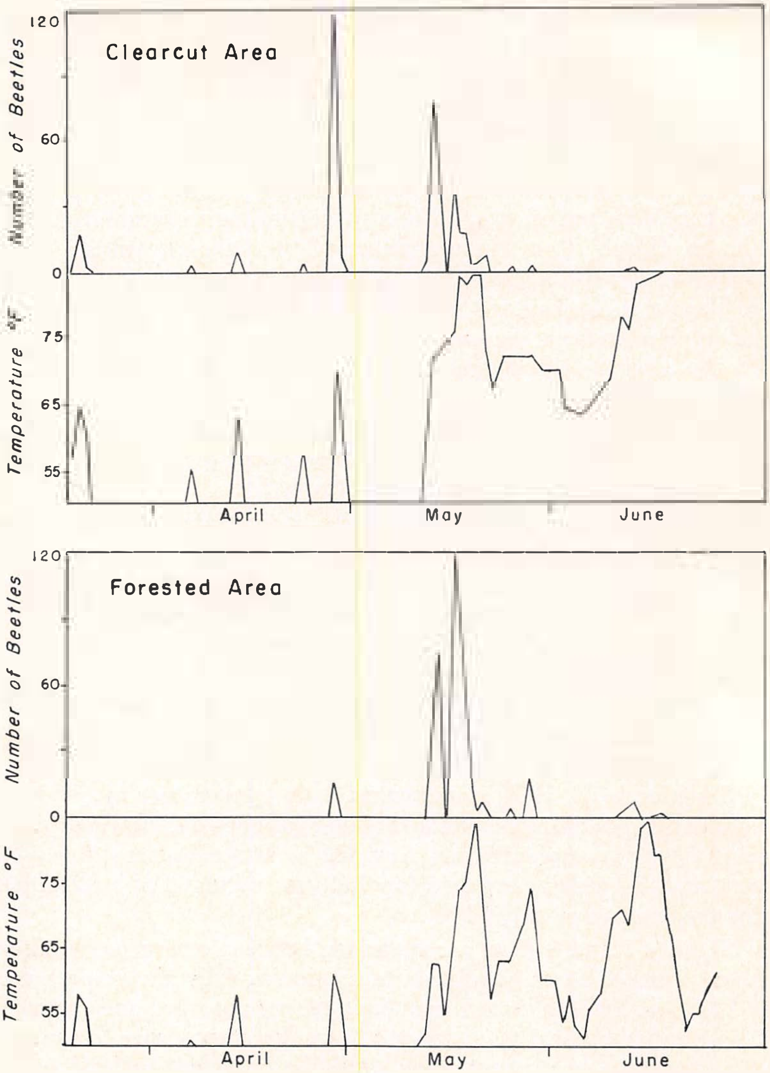

Figure 3. Emergence of *Dendroctonus pseudotsugae* Hopkins from clearcut and forested areas in relation to maximum daily air temperatures in 1963.

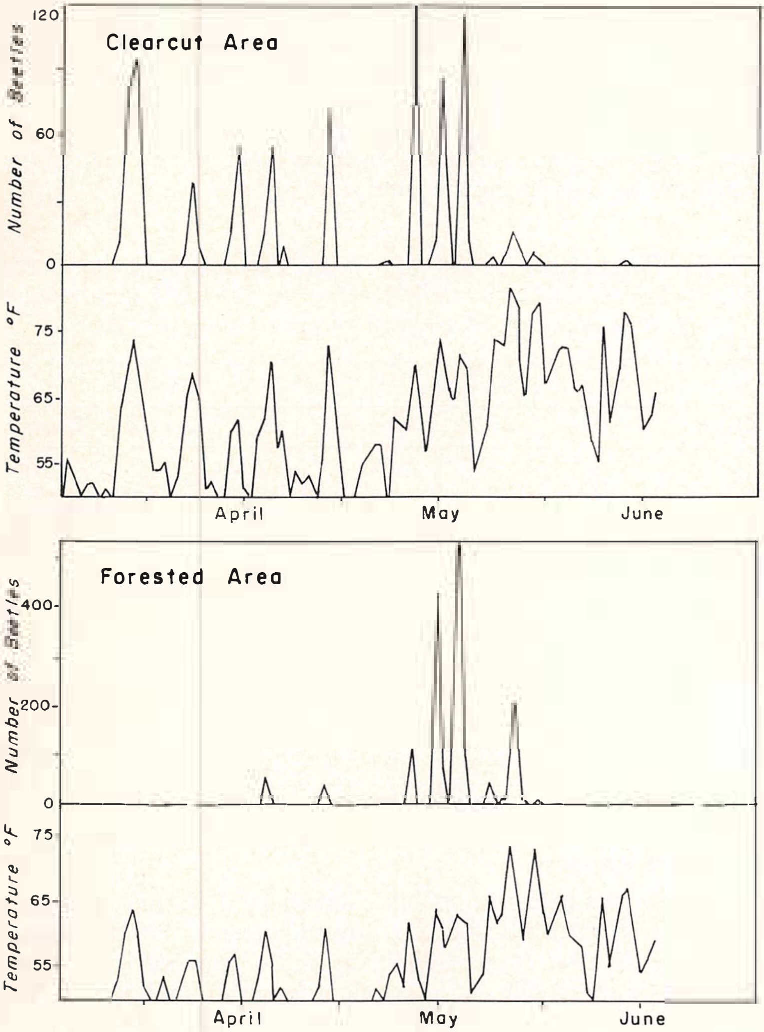

Figure 4. Emergence of *Dendroctonus pseudotsugae* Hopkins from clearcut and forested areas in relation to maximum daily air temperatures in 1964.

fect of radiation and heat absorption on development results in the early emergence in clearcut areas. Figures 3 and 4 show a seasonal emergence in clearcut areas occurring over a longer time period than that in the forested area and intermittently on those days when temperatures are still marginal in forested areas, resulting in a sporadic seasonal pattern. Local variations do occur from year to year and between different sites during the same year.

Table 2. Comparison of Air and Bark Temperatures in Clearcut and Forested Areas in Relation to Spring Emergence of *Dendroctonus pseudotsugae* Hopkins (May 16, 1963)

Hour	Clearcut			Forested		
	Air	Inner bark	Emerged	Air	Inner bark	Emerged
	° *F.*	° *F.*	*No.*	° *F.*	° *F.*	*No.*
0830	60	63	0	51	50	0
0900	61	70	0	54	51	0
1000	66	75	0	56	53	0
1100	70	86	6	58	54	4
1200	71	92	8	62	56	7
1300	71	97	6	65	57	8
1400	74	97	3	64	59	15
1500	77	104	7	65	60	21
1600	77	105	3	66	62	12
1700	72	90	2	65	61	11
1800	62	81	0	63	60	6
1900	56	74	0	60	59	3

Patterns of response

The Douglas-fir beetle exhibits a definite, well-defined sequence in its response to volatile attractants. Investigations in 1962 determined that during the first days of flight the beetle dispersal is at random when there is no freshly cut material in the area. On April 12, 1962, 117 Douglas-fir beetles were caught in nets and only 40 in baited olfactometers. Three days later, 164 beetles were collected from olfactometers, as compared to 16 in nets. This was not apparent in 1963, since beetles were caught in quantity on olfactory cages during the first day of flight, beginning a half-hour after sampling commenced. In 1964, however, 21 Douglas-fir beetles were collected in nets a day prior to any attraction response.

After the invasion of early female beetles, apparently directed flight alone occurs. Those beetles caught in rotating nets may be passing through the area in response to a distant attractant source.

Diurnal and seasonal patterns of response to attractants were found to be closely correlated with emergence. Figures 5 and 6 show the differences in seasonal patterns of Douglas-fir beetle response to attraction between 1963 and 1964. The patterns are very similar to those which resulted from seasonal net collections (Figure 7). Since the sequence of emergence, flight, and attraction represents a definite chain of events, the knowledge of factors influential in affecting flight is important. The occurrence of events as they relate to threshold temperatures is stressed. The physical factors of prime importance to flight are temperature, light, and wind. Other contributory factors include humidity, atmospheric pressure, and static electricity, not investigated in the present study. The combined effects of the environmental factors influence bark beetle activities and subsequent survival. Behavior patterns are governed by internal or external influences such as temperature, radiation, moisture, atmospheric pressure, vibration, light intensity and quality, contact and gravity, as well as chemical stimuli.

The greatest direct influences upon flight orientation are those stimuli which cause kinetic or directional responses. The importance of chemoreception is great as an influence in the discovery of both food and a mate. Chemotropic responses are either directed or nondirected. Directed responses are normally encountered in flight. Both responses, however, can be observed under laboratory and field conditions. These chemotropic responses result in four major effects: (1) arrestment, (2) stimulation, (3) attraction, or (4) repellent. In the case of the Douglas-fir beetle, these responses result in a sequence of reactions to various stimuli. Laboratory arrestment tests show that response depends upon whether the beetle is flying or crawling. Response to attraction requires air movement and therefore is usually restricted to flight. On the other hand, arrestment is exhibited only while crawling.

The Douglas-fir beetle is a univoltine insect and characteristically exhibits major flight activity during the spring and early summer. Once the temperature threshold for activity is reached and maintained, major activity occurs. Even with a gradual, constant increase in the overall temperature as the season progresses, the response patterns decrease. This tapering off in a seasonal attraction pattern results from the decrease in the amount of flying population. The duration of activity, however, is extended, due to reemerging beetles.

The impact of excessive fallen timber, which results from fire, wind, and logging, is apparent in the difference of population levels. During the summer of 1962, an endemic population of the Douglas-fir beetle existed near Corvallis, Oregon. Extensive downed timber as a result of the storm on October 12, 1962, caused a tremendous build-up

in brood adults the following season. During the fall and winter of 1963-64, a moderate amount of windthrow occurred; however, the supply was inadequate to absorb the massive population emerging in the spring of 1964. Consequently, outbreak conditions prevailed with a portion of the population invading standing trees.

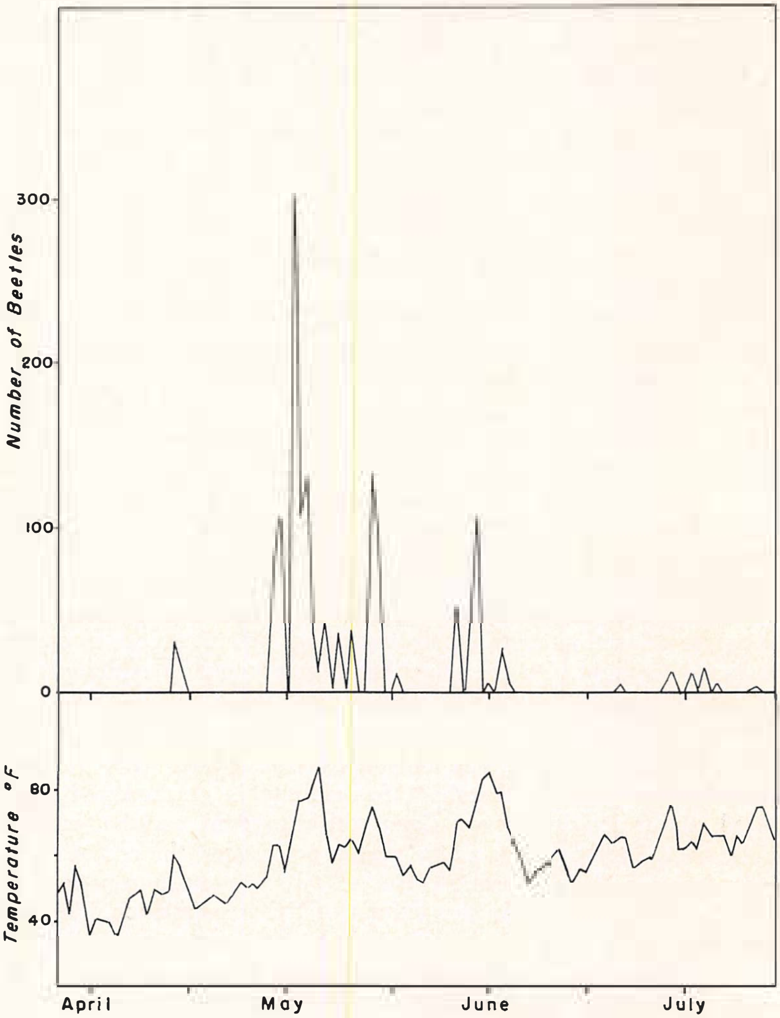

Figure 5. Seasonal pattern of attraction of *Dendroctonus pseudotsugae* Hopkins in relation to maximum daily air temperature, 1963.

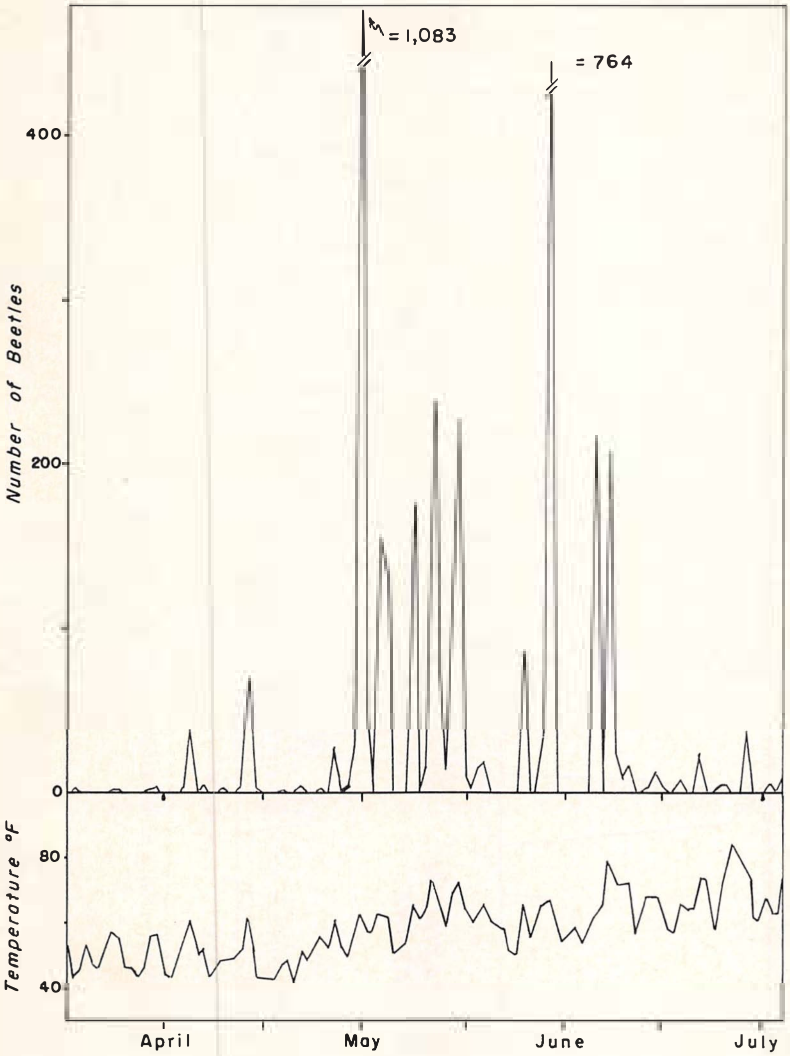

Figure 6. Seasonal pattern of attraction of *Dendroctonus pseudotsugae* Hopkins in relation to maximum daily air temperature, 1964.

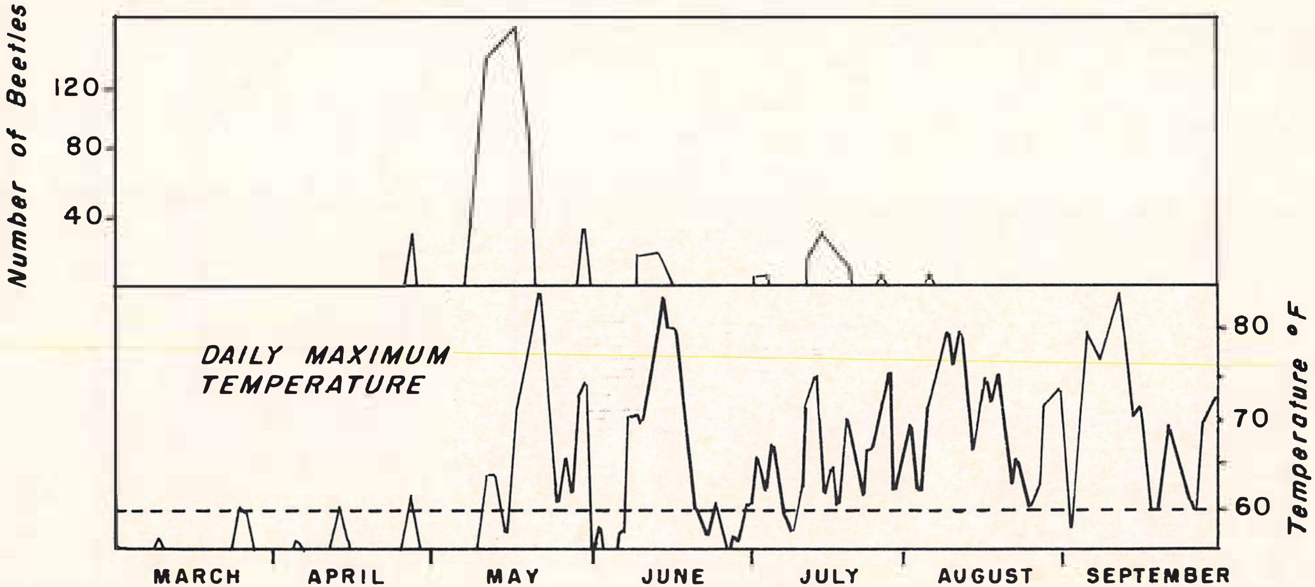

Figure 7. Seasonal pattern of *Dendroctonus pseudotsugae* Hopkins collected in nets during 1963 in relation to maximum daily air temperatures.

A vast increase in numbers occurred from 1963 to 1964. In 1963, 105 beetles were collected from one olfactometer during one hour, as compared to 824 in 1964. Figures 8 and 9 depict a variation in diurnal response for 1964 at various times throughout the season. The responses of flying beetles to baited olfactometers are closely related to temperature and light. The response patterns again resemble the diurnal patterns obtained from net collections on various days throughout the season.

Figure 8 shows that morning flight began at an air temperature of 58° F. on May 15, 1964. Rare cases of response were recorded at lower temperatures. On April 21, 1964, 21 Douglas-fir beetles were collected from attraction cages with an air temperature of 52° F. However, the recorded temperature in the clearcut area was 57° F., and undoubtedly flight was initiated in such areas from lower elevations and was later oriented into cooler temperature by attraction. Similarly, on April 24, 1964, under cloudy conditions, a limited number of beetles were collected from attraction cages in areas of 49° F.

In early spring, there is an increase in response with increase in temperature. April 28, 1964 (Figure 8), shows a flight pattern from noon until 1800 hours, with a peak at 1500 hours illustrating the tem-

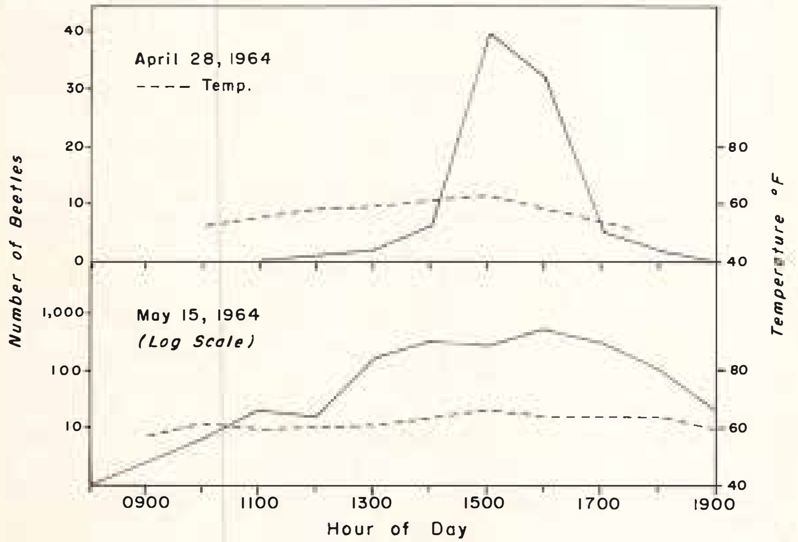

Figure 8. A comparison of typical diurnal attraction patterns of *Dendroctonus pseudotsugae* Hopkins in relation to maximum air temperature in April and May.

perature-dependent relationship. On May 15, 1964, flight occurred throughout the day from 0900 hours until after 1900 hours. It seems probable that once the flight threshold temperature has been reached, light intensity may be the important regulating factor, since the same general patterns result from either selective or net samples. A decrease was noted in flight numbers at 1500 hours on May 15 (Figure 8) when the peak temperature was reached. Since a temperature maximum of 66° F. would not be expected to cause a depression, light intensity may have caused this effect. The role of light with respect to optic orientation cannot be overlooked.

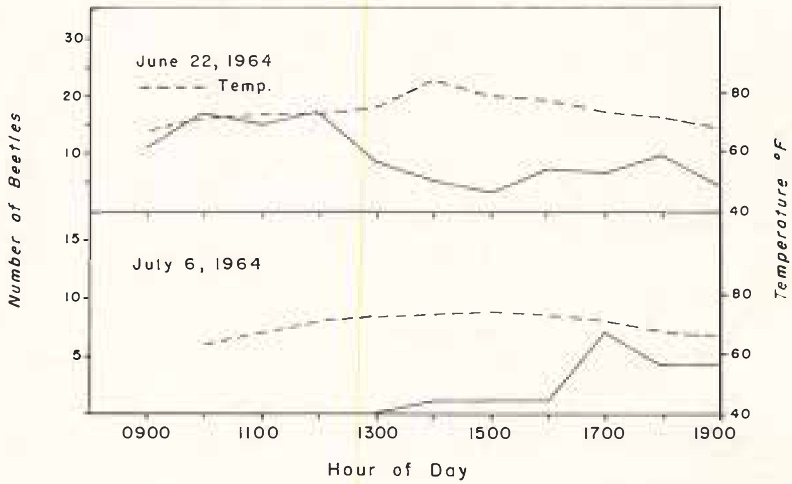

Figure 9. A comparison of typical diurnal attraction patterns of *Dendroctonus pseudotsugae* Hopkins in relation to maximum air temperature in June and July.

On June 22, 1964 (Figure 9), temperatures remained above the threshold level for flight throughout the daylight hours, and response occurred concurrent with an increase in light intensity. Considerable response occurred in the morning; however, an obvious midday depression began at noon as temperatures increased above 74° F. With a decrease in temperature and light intensity, a slight increase in beetle numbers again occurred. Toward the end of the season when field population was low and consisted mainly of reemerged beetles, this temperature-light effect was more apparent. The pattern on July 6, 1964 (Figure 9), represented a typical late season pattern where activity occurred only in mid-afternoon and early evening hours. Apparently the light intensity in July reaches its peak and is a factor or

co-factor together with temperature in influencing the change in flight and response patterns.

Attraction in various tree species

The fact that the unmated female Douglas-fir beetle also produces an attractant while feeding on phloem of various tree species was confirmed (*22*).

A correlation exists between attraction produced and subsequent attack and brood development. The highest number of attacks with successful brood development are on those species in which the females produce the greatest attraction.

Periodic counts of attacks on six different tree species (Douglas-fir, ponderosa pine, western white pine, western larch, grand fir, and western hemlock) were recorded from the beginning of the flight season until May 29, 1963. Of the six species placed outside the perimeter of an attraction center, only Douglas-fir and western larch sustained attack prior to May 29, whereas all species, except grand fir, within the perimeter of attraction were attacked. Grand fir was not attacked throughout the season on six replicates; the tree used had smooth bark and this may explain its escape, since attack on this species has been reported previously (*5*). On May 29, 1963, 10 unmated female beetles were manually introduced into the unattacked logs outside the attractant area. Attack occurred shortly thereafter on all species except grand fir in at least one of the replicates. Most galleries in hemlock and white pine were distorted and abnormal.

Attraction of reemerged beetles

Figure 5 shows that the bulk of response for 1963 occurred in mid-May. Thereafter, concurrent with inclement weather, little activity was apparent for a two-week period followed by a few days of limited activity as temperatures increased. In mid-July, 1963, there was additional activity undoubtedly as a result of beetles reemerging.

The attraction produced by reemerged females boring in Douglas-fir logs is considerably lower than that produced by virgin females; however, an attraction is produced which draws field population (Table 4). Although the level of attraction produced by reemerged females is low, the actual response of reemerged beetles to an attraction source is comparable to normal field population. In a release test on June 28, 1964, a response of 24% was obtained with marked reemerged beetles, as compared to 21% for field-responding beetles (those collected from attraction cages). An unknown percentage of the responding population during this time of the season was also reemerged beetles. Nevertheless, the test confirmed that reemerged beetles do respond.

Figure 10 shows that cage reemergence in 1963 occurred simultaneously with the flight activity recorded in mid-July (Figure 5). Activity for 1964 occurred concurrently with favorable weather beginning in mid-April and ending in July (Figure 6). A definite time of reemergence is difficult to denote; however, Figure 10 shows 1964 reemergence began the last part of May in caged logs. A change in sex ratio of beetles responding to attractant sources can be indicative of field reemergence. Table 3 shows the ratio of males to females which responded to female attraction. It is obvious that male response was greater from April through June, attaining a differential of 12 males to 1 female in 1964. Beginning in early July, there was a change to a higher percentage of female response, indicating that a high percentage of remaining field population in July was reemerged females. The sex ratio of males to females in caged reemerged beetles was one male to 1.3 females in 1963 with females predominating throughout the reemergence period. In 1964, a ratio of one male to 1.1 females was recorded, with a 1:1 pattern throughout most of the period and a slight increase in females during late June and early July.

Under heavy attack density in 1964, reemergence occurred almost continuously from late May through July. Obviously, the early part of this pattern (Figure 10) in 1964 was reemergence due to overcrowding. It was a search for more favorable oviposition sites rather than true reemergence that occurred in order to form a second brood, since reemergence began soon after entry and before any eggs were deposited. Under laboratory conditions, a high percentage of reemergence was obtained using an attack density of five females per square foot of bark surface area. In five log sections, an average of 73% reemergence occurred. The specific factors responsible for reemergence, however, are not included in this study.

Table 3. Comparison of Sex Ratio Change of *Dendroctonus pseudotsugae* Hopkins Responding to Attractants in 1963 and 1964

Year	Day of month													
	April	May						June				July		
	28	15	16	25	26	29	30	3	9	10	13	6	23	25
1963														
Male	2	..	2	2	..	5	..	6	..	2	2	1	..	1
Female	1	..	1	1	..	1	..	1	..	1	1	5	..	1
1964														
Male	2	2	..	..	2	..	9	12	4	..	2	1	1	..
Female	1	1	..	..	1	..	1	1	1	..	1	1	4	..

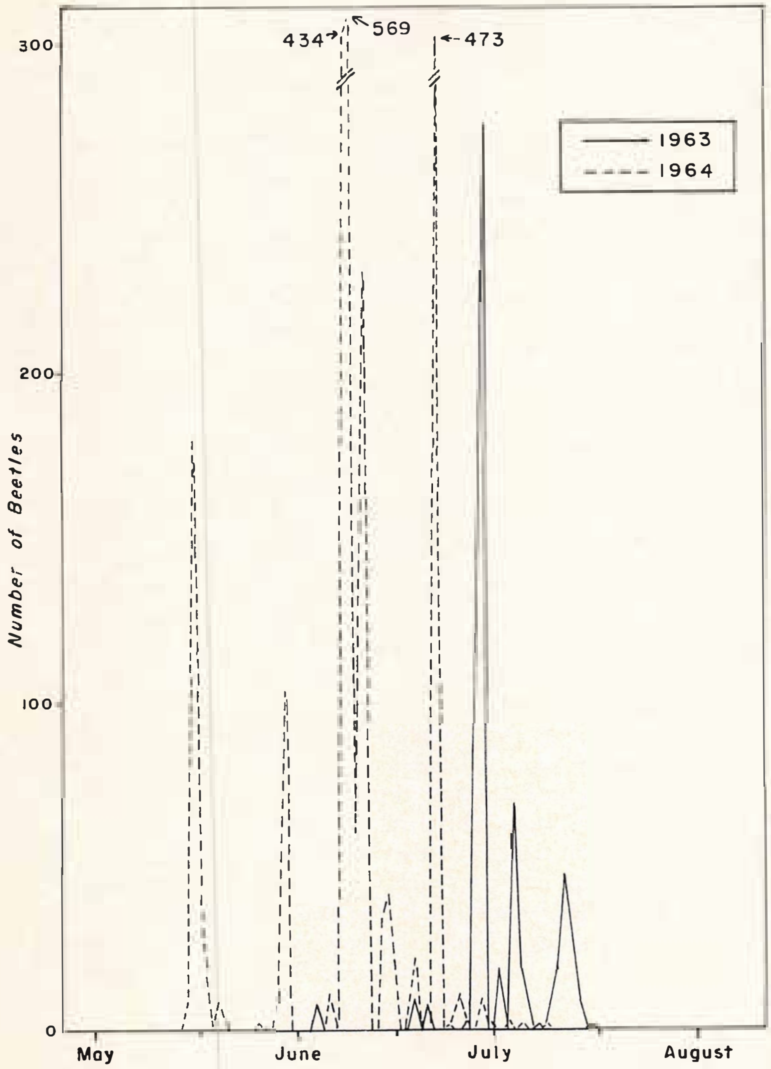

Figure 10. Reemergence patterns of *Dendroctonus pseudotsugae* Hopkins during 1963 and 1964.

Response to oleoresin compounds

Significant responses were obtained on oleoresin compounds during early season flight. Tables 4 and 5 compare the responses of field population to various sources of attractant materials. On April 28, 1964, 212 Douglas-fir beetles responded to 2½% Douglas-fir oleoresin. On April 19, 1964 (Table 5), four female beetles were collected from two olfactometers, one baited with 15%, the other with 25% oleoresin. Preliminary testing indicated (Table 5), in accord with findings in the literature (*7, 8*) and with laboratory results on arrestment, that field response would be highest at low resin concentrations. Testing of different percentages of Douglas-fir oleoresin indicated that 2½% was near the optimal concentration. Since the female Douglas-fir beetle initiates the gallery, the sex ratio of beetles which respond to oleoresin emphasizes the importance of its vapors in host finding. Out of 212 beetles attracted, 137 were females, a ratio of 1.8 females to one male. Table 3 shows a ratio of two male to one female response to the female attractant source on the same date. Males predominated in response to female-infested logs throughout the season, except during reemergence in July. On May 11, 1964, 80 beetles were attracted to Douglas-fir oleoresin and again females exceeded males in number. Subsequent to this date, although testing continued, little additional response to oleoresin was obtained, while response to secondary attraction continued (Table 4). This again denotes the importance of oleoresin in early season host finding.

Table 4 confirms that Douglas-fir beetles respond to fresh uninfested Douglas-fir logs, and the freshness of cut definitely regulates the responses obtained. Logs used prior to May 11, 1964, were cut on March 17 and had been stored in a walk-in cooler. No response to these logs was recorded when they were placed in the field. On May 11, two inches were cut from each end of one of the logs, and in addition, 40 blank holes were made in the bark to simulate attack. Immediate attraction resulted. Those replicates without fresh cuts or blank holes did not attract beetles (Table 4). Each time fresh holes were punched and/or new cuts were made, a few beetles could be attracted until late June. This effect would be similar to natural field conditions when oozing and volatilization of resin occurs due to injury or physiological stress.

The sex ratio of beetles responding to these uninfested logs was identical to that of beetles responding to the oleoresin, i.e., two females to each male, again indicating a superior capability of the female to find a host. The difference between the power of oleoresin and beetle attraction can be seen in Table 4. The superior power of the secondary beetle attraction is obvious. Considering that fresh cut logs are a source of oleoresin vapors, the data on May 15, 1964 (Table 4), em-

Table 4. SEASONAL ATTRACTION IN 1964 OF *Dendroctonus pseudotsugae* HOPKINS TO SOURCES OF DOUGLAS-FIR OLEORESIN AS COMPARED TO FEMALE-INFESTED LOGS

Date	Extracts: Oleoresin (2½%)	Extracts: Boring dust[1]	Logs: Fresh (uninfested)[2]	Logs: With virgin females	Logs: With reemerged females
	No.	*No.*	*No.*	*No.*	*No.*
March 30	--	--	--	7	--
April 7	--	--	--	3	0
8	--	--	--	1	2
13	--	--	--	2	0
14	0	--	0	5	0
18	0	--	--	1	0
19	--	--	0	86	3
21	--	--	0	8	0
24	--	--	0	2	0
28	212	--	0	120	0
May 3	--	--	0	2	0
6	--	--	0	6	0
11	80	--	(27)	539	23
14	--	--	(3)	102	8
15	--	--	(105)0	3,259	129
16	1	--	(2)0	126	18
18	--	--	0	215	88
23	0	--	--	349	42
26	5	--	(2)	323	56
27	--	(0)	0	137	2
28	--	--	0	21	0
29	0	--	--	128	--
30	0	--	(1)	228	1
31	--	--	0	8	0
June 2	--	--	0	12	0
3	--	--	0	18	0
12	--	--	0	46	0
13	5	109(0)	(7)0	1,984	0
20	0	(7)(5)	0	648	0
22	0	517	(7)0	262	--
24	0	20	0	19	--
29	0	--	(2)	30	--
July 6	0	7;21	--	36	--
19	0	--	--	8	--
23	0	--	--	3	--

[1] Parentheses indicate female dust extracts collected in water. Remaining replicates collected in ethyl alcohol.

[2] Parentheses indicate logs that were recut to expose fresh surface. The second number represents another replicate without fresh surface.

Table 5. Field Attraction During 1964 of *Dendroctonus pseudotsugae* Hopkins to Oleoresin Extracts and Fractions

Date	Douglas-fir Percent of oleoresin							Pine oleoresin fractions[1]				
	½	2½	5	15	25	50	100	myrcene	alpha pinene	beta pinene	limonene	check
	No.	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*
April 19	—	—	—	1	3	—	—	—	—	—	—	0
April 28	—	212	—	—	—	10	—	—	—	—	—	0
May 11	21	80	22	—	—	—	—	—	—	—	—	0
May 14	—	—	—	—	—	—	1	0	14	0	5	0
May 15	—	—	—	—	—	—	3	0	216	6	143	0
May 23	—	0	—	—	—	—	—	0	3	0	0	0
June 29	—	0	—	—	—	—	—	0	0	0	0	0
July 6	—	0	—	—	—	—	—	0	0	0	0	0

[1] Myrcene tested in benzene, other compounds diluted in ethyl alcohol. Pine fractions tested at 1% concentration. Checks included air, alcohol, and benzene.

phasize the quantitative difference between resin and beetle attraction. During early spring flight (April 28, 1964), attraction to 2½% oleoresin was higher than it was to the attraction of virgin female infested logs (Table 4).

The major question in host selection concerns random or oriented movements. In the case of the Douglas-fir beetle, as discussed above, the female beetle will attack other tree species located within the perimeter of an attractant source, indicating that attraction is to an area rather than to a specific tree.

Although the initial part of the dispersal flight of the Douglas-fir beetle is at random when no fresh windthrow is present, oriented responses begin early. The beetles are stimulated to flight by temperature and light or perhaps by odor later in the season, particularly when the temperature is marginal. Dispersal flight is usually oriented with the wind, in the absence of temperature effect. Once an attractant odor is encountered, the beetle orients its flight against the wind, indicating that air currents without a stimulation (pheromone or attractant) do not aid in orienting the beetle. Therefore, wind direction and velocity influence response patterns.

Considering that the sex ratio of beetles responding to oleoresin shows more females being attracted, the use of oleoresin in a control program could be timed for the most important period of spring flight. Thus, the pioneer females could be lured into a control area during the first few days or even hours after emergence begins within an area. Later in the seaeson, as activity continues, female-infested logs, producing the highly powerful secondary attraction, could be placed at strategic points throughout an area to draw the major portion of the flying population to predetermined traps.

Testing of individual fractions of pine oleoresin (Table 5) revealed that alpha pinene is the most attractive constituent in the oleoresin, followed by limonene, while only six beetles were caught on beta pinene.

In consideration of the results of all experiments described, a sequence in flight leading to location of suitable host can be visualized. Only in the absence of fresh windthrow or cut trees in the area is random flight possible for a brief period. If such fresh material is present, directed flight to resin vapors takes place from the beginning. As soon as the pioneer females bore into some trees, their boring allows additional resinous vapors to escape. Thus, directed flight can occur even before the secondary female attraction begins.

The first suitable log or weakened tree attacked in any infested area is the result of resin attraction. Subsequent attack of surrounding trees is the result of beetle attraction plus host or resin attraction

(vapors escaping from beetle entry holes). The beetle attraction, however, is substantially stronger.

Because a higher percentage of females than males are attracted by oleoresin compounds, the increased number of females produces a greater amount of secondary attraction in a shorter time. The result is "mass attraction" or true concentration flight. Under endemic population levels, however, the Douglas-fir beetle does not attack healthy standing trees in coastal areas. Therefore, it is considered as a secondary insect under those conditions, and mass attack is not essential for survival of the beetle in coastal areas; however, it concentrates attack on suitable host material. In contrast, in Rocky Mountain areas the Douglas-fir beetle does attack living trees, although a portion of these may be physiologically weakened due to drought conditions. Also, under outbreak conditions in coastal areas, attack will spread into standing trees, and again a concentration of beetles is essential to survival, since a few isolated beetles boring in a living tree cannot overcome its resistance.

Injury not only adds stress to the tree but enhances its attractiveness by creating an avenue of escape for oleoresin, as shown in the present studies by attraction attained on uninfested Douglas-fir logs simply by punching holes in the bark or by making fresh end cuts. Tests confirmed that Douglas-fir beetles do respond to fresh uninfested Douglas-fir logs, and freshness of cut definitely regulated the responses obtained. The sex ratio of two females to one male which responded to oleoresin compounds and to fresh cut logs indicates the importance of oleoresin vapors in host selection, since the female initiates the gallery. In general, the sex ratio of emerging beetles was one to one, and the ratio responding to a female-infested log was two males to one female.

Oleoresin functions as an attractant in one respect, while acting as a repellent at other times. Even a low concentration of oleoresin will repel beetles in close proximity to it. At high concentrations the oleoresin is toxic, yet, having been diluted by air, remains attractive to the flying population.

Effects of mating on attraction

Table 6 records the effect of mating on Douglas-fir beetle attraction. Early investigations in 1962 showed a limited response of field population to those logs with introduced pairs during the first four to six hours after introduction, but attraction stopped after all females were mated (*35*). Current investigations confirm the immediate drop-off in numbers attracted by boring females after mating (Table 6). Those mated early in the morning, before flight of field population had started, remained nearly nonattractive all day, while check samples continued to show the expected diurnal pattern of response.

Table 6. Field Attraction During 1964 of *Dendroctonus pseudotsugae* Hopkins to Mated Females Boring in Douglas-fir Logs

Time of mating	Hour of day												Following day
	8	9	10	11	12	13	14	15	16	17	18	19	
	Number of beetles												
May 23													
0430	–	–	0	1	2	0	0	1	0	0	0	–	1
Check	–	–	0	1	11	55	153	74	38	15	2	–	16
May 26													
0630	0	1	0	2	0	0	0	2	1	0	0	0	0
0800	4	2	3	4	1	0	0	2	1	0	0	0	0
1130	6	3	5	38	8	7	2	4	1	2	1	0	0
Check	1	3	13	18	14	23	43	118	95	23	16	1	137
May 30													
1000	6	10	55	4	1	1	1	0	0	–	–	–	0
Excised females[1]													
Log No. 1	0	0	0	3	2	8	18	18	12	–	–	–	–
Log No. 2	0	0	0	2	2	4	18	8	12	–	–	–	–
Log No. 3	0	0	0	0	0	2	12	13	7	–	–	–	–
Check	0	2	17	16	17	44	32	51	49	–	–	–	–

[1] Females mated on May 26 were excised on May 30 and reintroduced into fresh logs to test for subsequent attraction.

Females from three logs were excised on May 26, 1964, after mating and reintroduction into fresh Douglas-fir logs. These females again began to produce a low level of attraction in comparison with virgin females. This attraction did not originate from the fresh log with newly punched holes, since Table 4 shows virtually no attraction response for that time of the season to either a fresh uninfested log or to a low concentration of oleoresin. Therefore, results confirm that these mated females, once removed from the males, do attract again, indicating that not only initial mating but also presence of the male is necessary to curtail attraction. It is not known whether repeated periodic mating or simply the packing of the gallery with frass and borings eliminates the escape of volatile substances, but the latter seems unlikely since the level of attraction drops so rapidly after introduction of the males. Sufficient packing could hardly have occurred. Disturbance by handling undoubtedly causes slight effect; however, at various times throughout the season, female-infested logs received considerable rough treatment, yet similarly handled unmated females produced high attraction within minutes after the log was left undisturbed. Since the level of attraction drops so suddenly atfer the male enters the female gallery, the female apparently stops producing attractant at once. In addition, either the substance is produced externally or it is extremely volatile, since very little residue remains in the frass.

Experiments with female boring extracts collected in the laboratory and later tested in the field also suggest volatility. Table 4 shows very little attraction to dust extracts collected in water as opposed to those collected in ethyl alcohol, indicating that the attractant is too volatile to be retained in water, or perhaps it is insoluble in water. Callow adult males, taken from galleries prior to diapause and placed in galleries of highly attractive virgin females, caused the same immediate drop-off in numbers of field population attracted. Attraction, however, remained higher than on those mated with mature males and equaled attraction of check samples on the following day. Callow adult females excised from logs prior to diapause and introduced manually into Douglas-fir logs failed to attract field populations. These females did arrest male beetles in laboratory studies in some instances, although consistent results could not be duplicated and arrestment depended upon age of the females used.

SUMMARY

This study entailed the investigation of the behavioral responses exhibited by the Douglas-fir beetle, *Dendroctonus pseudotsugae* Hopkins, to various attractant sources. Tests were designed to observe olfactory responses, and results were later compared with collections from the sampling nets and with emergence patterns.

Laboratory tests revealed that the attractant produced by females when boring in both host and nonhost logs arrested adult beetles.

A histological study of various stages of both male and female digestive tracts was made.

The finding that the unmated female produces an attractant while feeding on phloem of various tree species was confirmed. The Douglas-fir beetle attraction is considered to be species specific, and both sexes respond to it. Significant responses were obtained using low concentrations of oleoresin compounds and pine oleoresin fractions. Largest responses occurred on 2½% Douglas-fir oleoresin. Tests with fractions of pine oleoresin showed that alpha pinene was the most attractive constituent, followed by limonene.

Behavior while crawling differs between sexes. Females continue to disperse and find a suitable site to initiate a gallery, while males are arrested by boring females.

Investigations confirmed a sudden decrease in the number of beetles attracted immediately after mating. Reemerged female beetles making their second or summer attack again exhibited considerable attraction even though they had been mated earlier.

REFERENCES CITED

1. Anderson, Roger F. 1948. Host selection by the pine engraver. Jour. Econ. Ent., *41:* 596-602.
2. Atkins, M. D. 1959. A study of the flight of the Douglas-fir beetle *Dendroctonus pseudotsugae* Hopk. (Coleoptera :Scolytidae) I. Flight preparation and response. The Can. Entom., *91:* 283-291.
3. Bedard, W. D. 1933. The Douglas-fir beetle—Its seasonal history, biology, habits and control. Coeur d'Alene, Idaho: USDA, Department of Entomology, Forest Insect Field Station. (Unpublished report.)
4. Chamberlin, W. J. 1939. *The Bark and Timber Beetles of North America North of Mexico.* Corvallis: Oregon State College Cooperative Association, 513 pp.
5. Chamberlin, W. J. 1958. *The Scolytoidea of the Northwest.* Corvallis: Oregon State College, 208 pp.
6. Chapman, J. A. 1954. Flight of *Dendroctonus pseudotsugae* in the laboratory. Canada Department of Agriculture, Forest Biology Division, Bimonthly Progress Rept., *10*(4) : 4.
7. Chararas, C. 1958. Role attractif de certains composants des oléorésines à l'égard des Scolytidae des résineux. Acad. Sci., Paris, *247*(19) : 1653-1654.
8. Chararas, C. 1959. L'attractivité exercée par les conifères à l'égard des Scolytides et le role des substances terpéniques extraites des oléorésines. Revue de Pathologie Végétale et d'Entomologie Agricole de France, *38:* 113-129.
9. Chararas, C., and A. Berton. 1961. Nouvelle methode d'analyse des exhalaisons terpéniques de pinus Maritima et comportement de *Blastophagus piniperda* (Coleoptera :Scolytidae). Revue de Pathologie Végetâle, *40*(4) : 235-243.
10. Daterman, Gary E. 1964. Diurnal and seasonal flight patterns of bark beetles (Coleoptera :Scolytidae) associated with Douglas-fir forests of western Oregon. Master's thesis, Corvallis: Oregon State University, 110 numb. leaves.
11. Dethier, Vincent G. 1947. *Chemical Insect Attractants and Repellents.* Philadelphia: Blakiston, 289 pp.
12. Gara, Robert Imre. 1962. A field approach to study of the flight behavior of bark beetle populations (Coleoptera :Scolytidae). Master's thesis, Corvallis: Oregon State University, 93 numb. leaves.
13. Gibson, Archie L. 1957. Tests of bark-penetrating insecticides to control the Douglas-fir beetle. Jour. of Econ. Ent., *50:* 266-268.
14. Graham, Kenneth. 1959. Release by flight exercise of a chemotropic response from photopositive domination in a scolytid beetle. Nature, *184:* 283-284.
15. Green, Nathan, Morton Beroza, and Stanley A. Hall. 1960. Recent developments in chemical attractants for insects. Advances in Pest Control Research, *3:* 129-179.
16. Hendrickson, W. H. 1965. Certain biotic factors influencing the invasion and survival of the Douglas-fir beetle, *Dendroctonus pseudotsugae* Hopkins (Coleoptera :Scolytidae) in fallen trees. Ph.D. thesis, Corvallis: Oregon State University, 179 numb. leaves.

17. Hopkins, A. D. 1893. Damage to forests by the destructive pine bark beetle. USDA, Bureau of Entomology, Insect Life, *5:* 187-189.

18. Hopkins, A. D. 1916. Economic investigations of the scolytid bark and timber beetles of North America. USDA, Program of Work of the U. S. Dept. of Agriculture 1916/1917, p. 353.

19. Jacobson, Martin, and Morton Beroza. 1963. Chemical insect attractants. Science, *140* (3574) : 1367-1373.

20. Jacobson, Martin, and Morton Beroza. 1964. Insect attractants. Scientific American, *211* (2) : 20-27.

21. Jantz, Orlo K., and Richard L. Johnsey. 1964. Determination of sex of the Douglas-fir beetle *Dendroctonus pseudotsugae* Hopkins (Coleoptera: Scolytidae). The Can. Entom., *96:* 1327-1329.

22. Jantz, Orlo K., and J .A. Rudinsky. 1965. Laboratory and field methods for assaying olfactory responses of the Douglas-fir beetle *Dendroctonus pseudotsugae* Hopkins. The Can. Entom., *97* (9) : 935-941.

23. Johnson, Norman E. 1960. Douglas-fir beetle: A problem analysis. Centralia: Weyerhaeuser Timber Company, Forestry Research Note 29.

24. Johnson, N. E., and L. F. Pettinger. 1961. Douglas-fir beetle attack in living trees as influenced by the presence of fresh windthrow. Centralia: Weyerhaeuser Timber Company, Forestry Research Note 27.

25. Karlson, Peter, and Adolf Butenandt. 1959. Pheromones (ectohormones) in insects. Ann. Rev. of Ent., *4:* 39-58.

26. Kinghorn, J. M. 1955. Chemical control of the mountain pine beetle and Douglas-fir beetle. Jour. of Econ. Ent., *48:* 501-504.

27. Kurth, Ervin F. 1952. The extraneous components of wood. In: *Wood Chemistry,* Louis E. Wise, ed., New York: Reinhold, pp. 385-445.

28. LeConte, John I., and George H. Horn. 1883. Classification of the coleoptera of North America. Smithsonian Miscellaneous Collections: Vol. 26, publication no. 507, Washington, D. C.: Smithsonian Institution, 567 pp.

29. McCowan, Vaughan F., and Julius A. Rudinsky. 1954. Biological studies on the Douglas-fir bark beetle. Centralia: Weyerhaeuser Timber Company, Forestry Research Note, Progress Report.

30. McMullen, L. H., and M. D. Atkins. 1961. Intraspecific competition as a factor in the natural control of the Douglas-fir beetle. Forest Science, *7:* 197-203.

31. McMullen, L. H., and M. D. Atkins. 1962. On the flight and host selection of the Douglas-fir beetle *Dendroctonus pseudotsugae* Hopk. (Coleoptera: Scolytidae). The Can. Entom., *94:* 1309-1325.

32. Pitman, G. B., and J. P. Vité. 1963. Studies on the pheromone of *Ips confusus* (Lec.) I. Secondary sexual dimorphism in the hindgut epithelium. Contributions from Boyce Thompson Institute, *22:* 221-226.

33. Pitman, G. B., R. A .Kliefoth, and J. P. Vité. 1965. Studies on the pheromone of *Ips confusus* (LeConte). II. Further observations on the site of production. Contributions from Boyce Thompson Institute, *23:* 13-17.

34. Rudinsky, J. A. 1961. Developments in forest pest research at Oregon State University. *In:* Proceedings of the Annual Meeting of the Western Pest Committee, Portland, Oregon, pp. 14-15.

35. Rudinsky, J. A. 1963. Response of *Dendroctonus pseudotsugae* Hopk. to volatile attractants. Contributions from Boyce Thompson Institute, *22:* 23-38.

36. Rudinsky, J. A. 1966. Host selection and invasion by the Douglas-fir beetle, *Dendroctonus pseudotsugae* Hopkins, in coastal Douglas-fir forests. The Can. Entom., *98:* 98-111. 1966.
37. Rudinsky, J. A., and J. P. Vité. 1959. Certain ecological and phylogenetic aspects of the pattern of water conduction in conifers. For. Sci., *5:* 259-266.
38. Smith, R. H., 1963. Toxicity of pine resin vapors to three species of *Dendroctonus* bark beetles. Jour. of Econ. Ent., *56:* 827-831.
39. Snodgrass, R. E. 1935. *Principles of Insect Morphology.* New York: McGraw-Hill, 667 pp.
40. Vité, J. P. 1961. The influence of water supply on eleoresin exudation pressure and resistance to bark beetle attack in *Pinus ponderosa.* Contributions from Boyce Thompson Institute, *21*(2) : 37-66.
41. Vité, J. P., and R. I. Gara. 1961. A field method for observation on olfactory responses of bark beetles (Scolytidae) to violatile materials. Contributions from Boyce Thompson Institute, *21:* 175-182.
42. Vité, J. P., and R. I. Gara. 1962. Volatile attractants from ponderosa pine attacked by bark beetles (Coleoptera:Scolytidae). Contributions from Boyce Thompson Institute, *21:* 251-273.
43. Vité, J. P., and J. A. Rudinsky. 1962. Investigations on the resistance of conifers to bark beetle infestation. Transactions of the 11th International Congress for Entomology, Vienna, 1960, *2*(sec. 7/14) : 219-225.
44. Vité, J. P., and David L. Wood. 1961. A study of the applicability of the measurement of oleoresin exudation pressure in determining susceptibility of second growth ponderosa pine to bark beetle infestation. Contributions from Boyce Thompson Institute, *21*(2) : 67-78.
45. Wilson, Edward O. 1963. Pheromones. Scientific American, *208*(5) : 100-114.
46. Wood, David L. 1962. The attraction created by males of a bark beetle *Ips confusus* (Lec.) attacking ponderosa pine (Coleoptera:Scolytidae). The Pan-Pacific Entom., *38:* 141-145.
47. Wood, David L., and J. P. Vité. 1961. Studies on the host selection behavior of *Ips confusus* (Lec.) (Coleoptera:Scolytidae) attacking *Pinus ponderosa.* Contributions from Boyce Thompson Institute, *21:* 79-95.